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EFFECT OF DOWNY MILDEW ON PRODUCTIVITY OF SUGAR BEETS, AND SELECTION FOR RESISTANCE[1,2]

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INTRODUCTION

FOR MANY YEARS downy mildew has been recognized as a serious disease of sugar beets in the coastal regions of California during seasons when climatic conditions favored the development of the fungus. Farther inland, before 1935, this disease was considered of only minor importance; but in 1935, 1936, and 1937 there were serious epidemics over wide areas in the lower Sacramento Valley.

This disease, caused by *Peronospora schachtii* Fuckel, has been known in Europe since 1852, but was first reported in the United States by R. E. Smith and E. H. Smith (*7*)[4] in 1911. During subsequent seasons downy mildew appeared sporadically in the coastal sugar-beet-producing areas. In 1926 and 1927 Bensel[5] reported severe outbreaks in the Santa Clara Valley. Since 1930 the disease has appeared regularly in the Salinas Valley of Monterey County, the Santa Maria Valley of Santa Barbara County, and in Ventura and Orange counties. There were destructive outbreaks in the Salinas Valley in 1930, 1937, and 1938; moderate epidemics during other seasons. According to a 1937 survey by Mr. Suttie of the Spreckels Sugar Company, covering 3,721 acres, about 22 per cent of the beets were infected by the middle of June. In 1938, up to 80 per cent of the beets were infected in some fields in the Salinas Valley.

The same fungus frequently ruins garden beets grown for the market or for seed, as in 1929, when 40 per cent of the seed crop in the Sacramento Valley

[1] Received for publication September 28, 1943. The field experiments reported in this paper were made possible through financial contributions by the beet-sugar companies operating in California. The project on the selection of sugar beets for resistance to downy mildew was discontinued at the end of the 1940 season; and, with the consent of the sugar companies, all materials that appeared to be of value for further testing or selection were made available to the United States Department of Agriculture, Office of Sugar Plant Investigations, for incorporation in their project on sugar-beet improvement.

[2] The writer wishes to thank M. W. Gardner and J. B. Kendrick for advice during the investigations and the preparation of the manuscript, and to acknowledge assistance in part of this work from B. R. Houston, H. Rex Thomas, Wayne F. Weeks, and David N. Wright.

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[4] Italic numbers in parentheses refer to "Literature Cited," at the end of this paper.

[5] Bensel, G. E., 1927. Mildew of sugar beets (*Peronospora schachtii* Fuckel). Unpublished report. Spreckels Sugar Company, Dept. Agr. Res. Rept. 2:19–21.

was destroyed (*4*). Downy mildew has also been reported on garden beets in Oregon and Washington and observed at times on sugar beets in Colorado.

Though small plants may be killed by a severe infection of downy mildew, this disease is rarely fatal to sugar beets past the thinning stage. Under certain conditions, secondary organisms gain entrance through leaves killed by the mildew, and rot the crown or the entire root. High temperature seems especially favorable for this secondary decay. The direct effects of the fungus on the plant are usually of greater importance. Infected leaves are malformed and smaller, but often more numerous than the leaves on normal plants. Because the infection is systemic in the growing point, there is complete infection of all the new heart leaves formed while conditions favor the fungus. Often new growing points are established on the periphery of the crown; the result

TABLE 1

EFFECT OF DOWNY MILDEW ON THE PRODUCTIVITY OF SUGAR BEETS, SALINAS, 1930*

	Average root weight, pounds	Sucrose, per cent	Purity, per cent	Relative yield	
				Root weight	Indicated available sugar†
Noninfected beets	3.13	13.5	83.8	100.0	100.0
Infected beets	2.43	11.5	77.3	77.6	61.0
Difference	0.70	2.0	6.5	22.4	39.0
Significant difference, odds 19:1	0.38	1.16	3.07	....	....

* Planted December 1, 1929; harvested July 17, 1930.
† Assuming 100 per cent extraction. Obtained by multiplying yield by sucrose per cent by purity per cent.

is irregularly shaped roots and a divided crown. Some crowns are hollow because of the unequal growth; these, together with the killed leaves, provide openings for secondary organisms. Most of the infected plants recover from the infection with the advent of dry, warm weather and grow almost normally; but a number remain permanently stunted. In the opinion of growers and sugar-company officials, not only is the yield strikingly reduced by the infections, but the sucrose per cent and the apparent purity of beets from mildewed fields is also lower than from disease-free fields, a condition that interferes seriously with sugar extraction.

Control of downy mildew on sugar beets by fungicidal sprays or dusts does not appear practicable at present. The sporadic appearance of the outbreaks, the partially systemic nature of the infection in the plant, and the long periods during which protection would be necessary contribute to the difficulties of fungicidal control. Apparently, therefore, the use or development of resistant varieties or strains of beets for areas where downy mildew is prevalent would be the most satisfactory solution; this topic is further discussed in a later section of this paper.

EFFECT OF DOWNY MILDEW ON YIELD

Before the present series of experiments was inaugurated, two trials (*5*) had been conducted to determine how downy mildew affects the size and the yield of sugar beets. In each trial—one at Salinas, California, in 1930 and one

near Davis in 1935—the sugar beets in nine plots were separated into diseased and healthy groups, and yield determinations were made on each lot. At Salinas each plot consisted of 100 nonbolting beets growing consecutively in a single bed. The segregation into diseased and healthy groups was made entirely on the basis of downy-mildew symptoms at harvest time, July 17.

As table 1 indicates, the average root weight, sucrose per cent, and apparent purity of the beet juices were significantly lower in the diseased than in the healthy beets. According to these data, downy-mildew infection reduced the yield of roots by 22 per cent and the indicated available sugar by 39 per cent in comparison with noninfected plants in the same plots.

Because at harvest it is often difficult to determine whether or not beets had at some time been infected by downy mildew, the record of infected plants in

TABLE 2

EFFECT OF DOWNY MILDEW ON THE PRODUCTIVITY OF SUGAR BEETS, DAVIS, 1935*

	Average root weight, pounds	Sucrose, per cent	Purity, per cent	Relative yield	
				Root weight	Indicated available sugar†
Noninfected beets	2.27	15.7	87.5	100.0	100.0
Infected beets	1.72	14.3	83.7	75.8	66.0
Difference	0.55	1.4	3.8	24.2	34.0
Significant difference, odds 19:1‡	0.48	n.s.	n.s.	....	....

* Planting date not determined; harvested September, 1935.
† Assuming 100 per cent extraction. Obtained by multiplying yield by sucrose per cent by purity per cent.
‡ The abbreviation n.s. indicates that differences are not significant.

the plots at Davis in 1935 was made on May 20. Observations showed that in this locality there was no spread of downy mildew in the plots after this date. At harvest time (September) the plants previously recorded as infected in each of the nine test rows were segregated from the disease-free plants. As yield data (table 2) reveal, plants not affected developed significantly larger roots than infected plants. The average sucrose per cent and the purity of the healthy plants appeared greater than those of the diseased; but, in this test, the differences were not statistically significant.

Trials at Santa Maria in 1937.—During the spring of 1937, sugar beets were planted at Santa Maria, in coöperation with the Union Sugar Company in order to determine further the effect of downy mildew on the yield of sugar beets and to observe the relative susceptibility of some commercial varieties. Nine varieties were planted in 4-row plots, 100 feet long, and were replicated five times in randomized blocks. Observations were made at intervals of 2 weeks from the time mildew was first observed until near the date of harvest. At each observation the newly infected plants were marked with a stake painted a distinctive color. At the end of the season, therefore, it was possible to segregate the infected beets in each plot according to the period during which mildew symptoms first appeared. Figure 1 shows the increase in per cent of plants infected during the growing season. The planting was made on March 5, and most of the infections were first evident during June. From 2 to 3

weeks is usually required from the time infection actually occurs until the systemic invasion of newly formed leaves can be observed. The period of most abundant infection, therefore, was about May 10 to June 15, when the beets were 65 to 100 days of age. This period coincided with a series of mornings characterized by high humidity, heavy dews, but no actual rainfall.

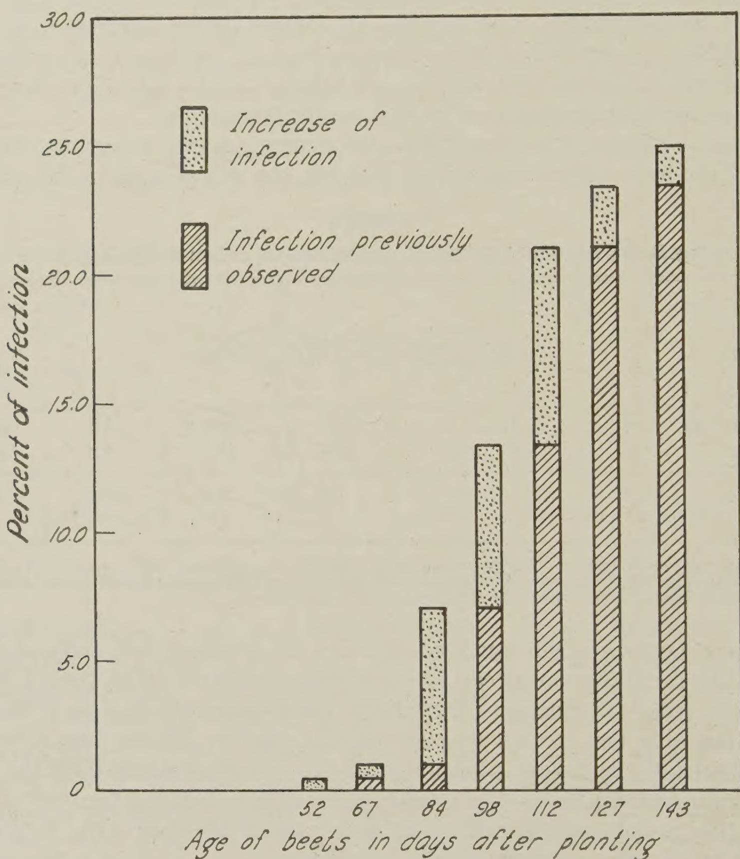

Fig. 1.—The increase of downy-mildew infection on sugar beets planted March 5, 1937, at Santa Maria. The greatest increases of infection were observed between May 28 and June 25, or 84 to 112 days after planting.

On August 17 to 19, when the plots were harvested, the beets first observed to be infected on each of the several dates of observation (fig. 2) were grouped, and their average root weight was determined. In general the results here indicate that the earlier the date of infection, the smaller the beet root at harvest time. An exception is noted in that the beets observed to be infected 52 days after planting show an average root weight about 0.3 pound heavier than the group observed to be infected 2 weeks later; but this difference may be due to experimental error, since the first group contained only a small number of infected roots. The other unusual feature is the fact that the groups of beets first observed to be infected as late as 127 and 143 days after planting

showed a higher average root weight than the nonmildewed beets. Actively growing beets are known to be more susceptible to downy mildew than slow-growing ones. In addition, since infection could first be detected only on systemically infected new growth, only the actively growing plants exhibited symptoms of infection. When the observations were made on July 10 and 26, symptoms of recent mildew infection were occurring almost exclusively on large, actively growing beets. Apparently, therefore—because of greater susceptibility or more active growth—there was a tendency for larger-than-average beets to be included in the infection groups during July.

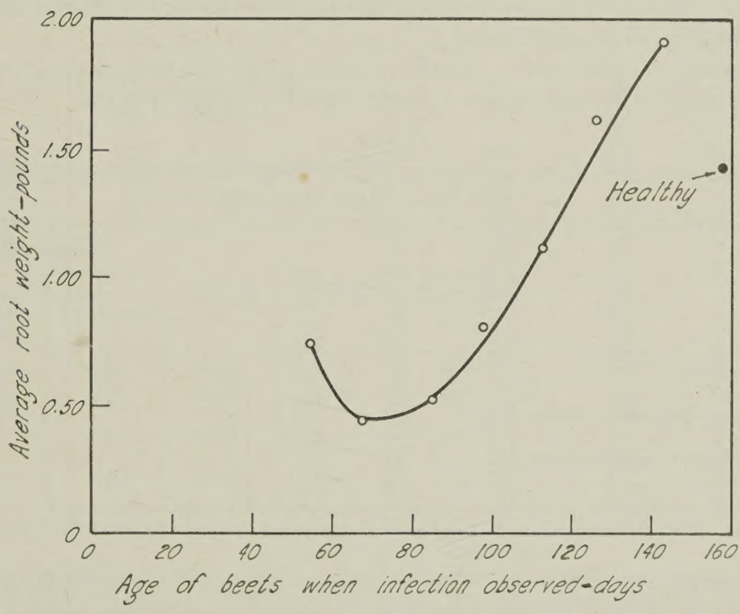

Fig. 2.—The relation between time of downy-mildew infection on sugar beets and the average root weight at harvest. Plants infected within 100 days of planting showed average root weights of less than 1 pound, whereas beets infected later exceeded this amount. Santa Maria, 1937.

To determine further the importance of earliness of infection, the beets were collected into three groups: early-infected plants upon which downy mildew was observed within 100 days after planting, late-infected plants which showed infection between 100 and 150 days after planting, and healthy or noninfected plants. Five samples were selected from each of the three groups in each of the nine varieties and were analyzed for sucrose and apparent purity. Each figure in table 3 represents, therefore, an average of 27 determinations.

As the table reveals, early-infected beets were less than half as large as healthy ones, whereas late-infected beets were nearly normal in size. The sucrose of both early- and late-infected beets was lower by 2 per cent than that of the noninfected. In the same way the average purity of both groups of infected beets was lower by 5 per cent than that of the noninfected beets in the same plots. The group infected between 100 and 150 days of age in-

cluded beets that were stunted by mildew infection and others that, because of vegetative vigor, weighed more than the average of noninfected beets. Both of these factors may have contributed to the lowered sucrose and purity. Perhaps the beets showing infection after 120 days of age were not adversely affected as to either yield or sugar production.

On the average, to judge from the relative yields shown in the last two columns of the table, the infected beets produced 72.6 per cent as much weight and 58.2 per cent as much sugar per plant as the noninfected. Whereas the late-infected group produced a nearly normal weight and 80 per cent as much sugar per plant as the healthy group, the yield of the early-infected was less than half that of the noninfected.

According to these results, downy mildew interfered with normal production by reducing the average root weight and the sucrose per cent. The death

TABLE 3

Effect of Early and of Late Downy-Mildew Infection on the Productivity of Sugar Beets, Santa Maria, 1937

	Average root weight, pounds	Sucrose, per cent	Purity, per cent	Relative yield	
				Root weight	Indicated available sugar*
Noninfected beets	1.35	17.77	81.92	100.0	100.0
Infected beets	0.98	15.42	76.10	72.6	58.2
Early-infected beets (prior to 100 days of age)	0.65	15.12	75.65	48.0	37.6
Late-infected beets (between 100 and 150 days of age)	1.32	15.58	76.29	97.6	79.4

* Assuming 100 per cent extraction. Obtained by multiplying yield by sucrose per cent by purity per cent.

of a considerable number of infected beets is still another factor that reduces productivity; and extraction of sugar is interfered with because of the reduced purity. Infections early in the life of the beet appear considerably more serious in relation to all these factors than are late infections.

Trials at Salinas in 1938.—During the season of 1938, a somewhat similar trial was conducted at Salinas in coöperation with the Spreckels Sugar Company. Ten varieties, some the same as in the previous trial, were planted in 4-row strips, 100 feet long, and replicated six times in randomized blocks.

The seed was planted on January 14; but because of cold, wet weather the plants grew very slowly and were not thinned until early in April. The first mildew count was made shortly after thinning, with later counts following at 2- or 3-week intervals until July 15. Detailed observations were made on only four of the ten varieties to secure additional information on the effect of the mildew and to permit comparison with the 1937 trials at Santa Maria. These four varieties were U.S. 14, U.S. 33, Hartmann, and R. & G. Old Type. At each interval the newly infected plants were distinguished with a colored stake, a different color being used at each interval. Thus at the end of the season the plants in each plot of these four varieties could be segregated into groups according to the period during which mildew symptoms were first observed. Figure 3 shows the increase in per cent of infection during the

growing season. The highest rate of increase in infection was observed between May 5 and June 3. Since 2 to 3 weeks usually elapses between infection and the expression of visible symptoms, apparently the most abundant infection occurred between April 15 and May 15, when the beets were 90 to 120 days of age.

The plots were harvested October 10 to 13; the infected beets in each of the four varieties were grouped according to their stake color, representing the date of infection; and the average root weight was determined for each group. As the results show (fig. 4), the earlier the date of infection, the lower the average root weight. In the groups that showed infection between 90 and 160

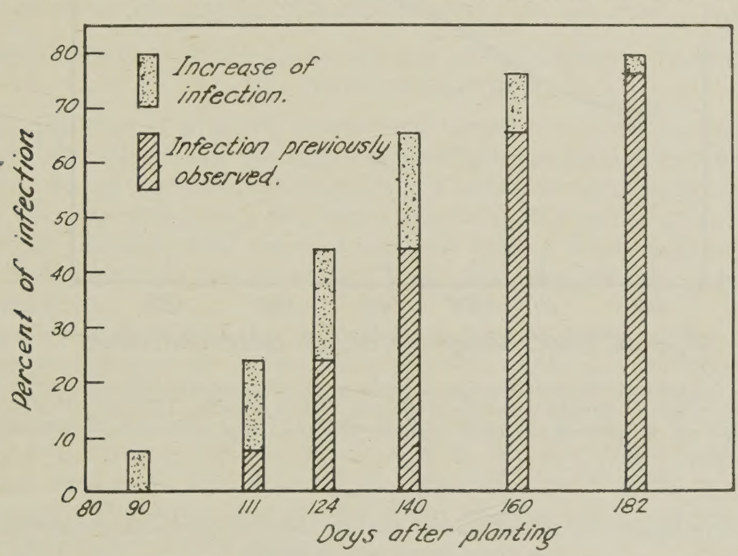

Fig. 3.—The increase of downy-mildew infection on sugar beets planted on January 14, 1938, near Salinas. The greatest increase of infection was observed between May 5 and June 3, or 111 to 140 days after planting.

days after planting, the average root weight for each successive infection group was 0.10 to 0.15 pound more than in the preceding group. The healthy beets show an average root weight 0.13 pound heavier than the beets observed to be infected at the 160- or 182-day interval, and approximately double the average root weight of those infected at the first observation.

To determine how infection at various stages of growth affected the sucrose per cent, the purity, and the yield, six composite samples were collected in each of the four varieties from beets infected prior to 125 days after planting, from beets infected after the 125-day interval, and from noninfected beets. These represented, respectively, early- and late-infected, and healthy groups.

Table 4 shows that early-infected beets were less than two thirds, late-infected beets over four fifths, as large as healthy beets. There was no appreciable difference between the sucrose per cent of the early- and the late-infected groups, and the healthy beets showed an improvement of only about 0.5 per cent over the infected. The coefficient of apparent purity differed very slightly between the infected and the noninfected groups.

On the average, according to the relative yields shown in table 4, the infected beets produced 73.64 per cent as much weight and 71.22 per cent as much sugar per plant as the noninfected.

In this trial, the main effect of downy-mildew infection was to reduce the average root weight of the infected beets and thus also to decrease the tonnage

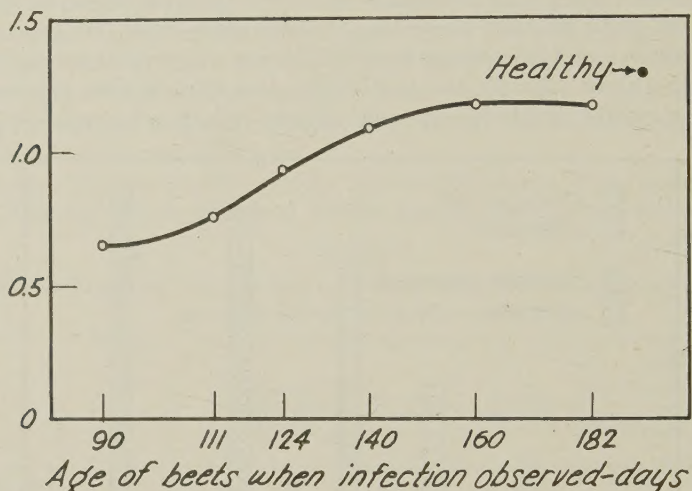

Fig. 4.—The relation between the age of beets when infection was first observed and the average root weight at harvest time. Beets showing infection within 125 days after planting gave average root weights of less than 1 pound, whereas beets infected later exceeded this amount. Salinas, 1938.

TABLE 4

EFFECT OF EARLY AND OF LATE DOWNY-MILDEW INFECTION ON THE PRODUCTIVITY OF SUGAR BEETS, SALINAS, 1938

	Average root weight, pounds	Sucrose, per cent	Purity, per cent	Relative yield	
				Root weight	Indicated available sugar*
Noninfected beets	1.29	18.27	87.74	100.00	100.00
Infected beets	0.95	17.72	87.49	73.64	71.22
Early-infected beets (prior to 100 days of age)	0.82	17.68	87.37	63.57	61.26
Late-infected beets (between 100 and 150 days of age)	1.11	17.76	87.61	86.05	83.52

* Based on 100 per cent extraction. Obtained by multiplying yield by sucrose per cent by purity per cent.

and the sugar production. Differences in purity and sucrose had very little influence in lowering of the total sugar production.

At Salinas the sucrose content and the purity were less affected by mildew than in the Santa Maria trials of the previous year. A possible reason is the difference in the harvesting dates of the two trials. As mentioned above, the greatest wave of mildew infection occurred at about the same dates in each trial, with infection falling off rapidly about the middle of July. Although the

Salinas plot was planted much earlier than the other, the thinning dates of the two were within a few days of each other. Since, however, the harvesting date at Santa Maria was 2 months earlier than at Salinas, the infected beets in the latter trial had 3 months after the mildew epidemic in which partially to recover and build up size, sucrose per cent, and purity, whereas those at Santa Maria were harvested before recovery could take place.

As indicated by the relative yields in tables 3 and 4, the weight of infected beets was about 27 per cent lower than that of noninfected beets at both Santa Maria and Salinas. The effect of downy mildew upon the indicated available sugar was, however, more pronounced in the Santa Maria trial because there the mildew caused a greater reduction in purity and in sucrose.

RELATIVE SUSCEPTIBILITY OF SUGAR-BEET VARIETIES TO DOWNY MILDEW

The planting of available commercial varieties that are resistant would seem to offer the simplest method of decreasing losses from downy mildew, but information on the relative susceptibility of varieties is extremely limited.

In France, Singalovsky (*6*) tested numerous beet varieties and reported that only two cultivated varieties remained free of downy-mildew infection and that the native species of wild beet, *Beta maritima* L., showed great susceptibility.

As previously stated, the 1937 trials at Santa Maria provided an opportunity to compare the susceptibility of nine sugar-beet varieties under a moderately severe natural epidemic of downy mildew. In this experiment (according to the per cent of infection shown in table 5), Hartmann and Eagle Hill were significantly less susceptible than the other varieties tested. Several, such as R. & G. Normal, R. & G. Old Type, U.S. 33, and U.S. 12, apparently fell into an intermediate group, whereas U.S. 14 proved to be the most susceptible of those tested.

As table 5 shows, the yield in tons per acre was in general greater for the varieties with a low or moderate per cent of infection. An exception is U.S. 14, which outyielded U.S. 12 and A-600 despite considerably higher infection. In sucrose per cent there were no significant differences except that Hilleshög, which produced a relatively low average root weight and tonnage, was exceptionally high in sucrose. The six varieties with the lowest per cent of infection showed, almost equally, the highest yield of gross sugar per acre, followed in order by U.S. 14, A-600, and U.S. 12. Since the differences in purity coefficients of the varieties were not significant, the yield of gross sugar per acre was a better measure of performance than the indicated available sugar.

From the weights, sucrose per cent, and purity of the healthy beets in each plot could be calculated the theoretical yield that would have been obtained from each variety in the total absence of downy mildew. Judging from these results, if the influence of mildew were eliminated there would be little difference between the sugar yields of the varieties except U.S. 12 and A-600, which appeared less productive under the conditions of these trials.

When the theoretical yields in the absence of mildew were compared with the actual yields, it was found that the 15 per cent mildew infestation on the

Hartmann variety reduced the yield by 0.7 ton of beets and 300 pounds of sugar per acre, whereas the 36 per cent infestation on U.S. 14 reduced the yield by 1.4 tons of beets and 730 pounds of sugar per acre. Other varieties showed losses intermediate between these figures, but in proportion to the percentage of infection.

The 1938 trials at Salinas provided an opportunity to compare the susceptibility of ten sugar-beet varieties under a very severe natural epidemic of downy mildew. According to the per cent of infection shown in table 6, the variety R. & G. AA, related to R. & G. Old Type, was significantly less susceptible than any of the others. It showed, however, a lower yield than several other varieties because it lacked uniformity in size and showed a relatively low sucrose per cent. Several commercial varieties such as Hartmann, Braune, U.S. 33, and R. & G. Old Type fell into an intermediate group, A-600 and U.S. 12 being somewhat more susceptible, and U.S. 14 the most susceptible of the varieties tested.

TABLE 5

SUSCEPTIBILITY TO DOWNY MILDEW, AND YIELD OF NINE SUGAR-BEET VARIETIES; SANTA MARIA, 1937*

Variety	Infected beets	Sucrose	Acre yield	
			Gross sugar†	Beets
	per cent	*per cent*	*pounds*	*tons*
Hartmann	15.1	17.26	5,930	17.19
Eagle Hill	16.9	17.38	5,640	16.21
Hilleshög	21.5	19.04	5,800	15.22
U.S. 33	22.5	17.19	5,460	15.87
R. & G. Normal	25.6	16.83	5,570	16.54
R. & G. Old Type	26.3	17.68	5,680	16.06
U.S. 12	26.4	17.06	4,340	12.70
A-600	30.6	17.18	4,810	14.00
U.S. 14	36.3	16.65	5,130	15.39
Significant differences:				
Odds 19:1	3.68	0.94	850	2.35
Odds 99:1	4.96	1.27	n.s.‡	n.s.

* Planted March 5, 1937; harvested August 17 to 19, 1937.
† Obtained by multiplying yield by sucrose per cent.
‡ The abbreviation n.s. indicates that the differences are not significant at the odds given.

The yield in tons per acre (table 6) indicates that the per cent of mildew infection was not the major factor involved in determining the tonnage produced. Two of the more susceptible varieties, U.S. 12 and A-600, showed the lowest yield; but U.S. 33, only moderately susceptible, yielded significantly lower than all others except the varieties mentioned above, whereas the yield of U.S. 14, the most susceptible variety, was significantly exceeded only by the highest-yielding variety. On July 15 the bolting per cent was highest in three of the domestic varieties, a fact that explains the lower yields of these varieties. Furthermore, the bolting in R. & G. Old Type, Hartmann, and U.S. 14 developed relatively late in the season and probably had little effect on the yield. U.S. 33, A-600, and U.S. 12 showed both the highest bolting and the

lowest average root weights of the ten varieties. It should be noted that this plot was planted on January 14 and was, therefore, particularly unfavorable for varieties with a high bolting tendency.

From the weights, sucrose per cent, and purity of the noninfected beets it was possible to calculate the theoretical yield that should have been obtained in the total absence of downy mildew from the four staked varieties. Judging from these results, downy mildew infestations of 62 to 80 per cent reduced the yield of sugar beets by 3.56 to 5.84 tons per acre, an average reduction of 20.3 per cent of the tonnage.

TABLE 6

SUSCEPTIBILITY TO DOWNY MILDEW, AND YIELD OF TEN SUGAR-BEET VARIETIES; SALINAS, 1938*

Variety	Mildew†	Bolting‡	Sucrose	Acre yield	
				Beets	Indicated available sugar
	per cent	*per cent*	*per cent*	*tons*	*pounds*
R. & G. AA	43.3	1.5	16.8	21.53	6,240
Hartmann	57.5	16.0	18.3	19.70	6,380
Braune	59.0	7.4	18.4	24.30	7,950
Braune (new type)	59.8	8.8	18.3	22.37	7,230
U.S. 33	62.0	41.4	17.2	14.76	4,450
R. & G. Old Type	62.2	15.6	18.3	19.60	6,340
Pioneer	63.0	6.4	18.7	19.39	6,410
A-600	66.9	40.8	16.4	12.69	3,590
U.S. 12	70.1	48.7	17.4	12.12	3,710
U.S. 14	79.9	13.6	17.7	21.22	6,510
Significant differences:					
Odds 19:1	4.37	2.38	1.07	1.63	505
Odds 99:1	5.84	3.18	1.43	2.17	675

* Planted January 14, 1938; harvested October 10 to 13, 1938.
† Percentage infection on June 3, 1938.
‡ Percentage on July 15, 1938.

A similar planting was made near Salinas in 1939. Nine varieties believed to be somewhat resistant to downy mildew or found relatively resistant in previous trials were replicated six times along with U.S. 14, known to be very susceptible. As table 7 shows, the lowest per cent of infection occurred upon U.S. 15, R. & G. AA, and R. & G. Old Type, although the infection on four other varieties was not significantly higher. Two varieties, R. & G. Old Type and U.S. 15, with low mildew infection and bolting, produced the highest yields by a wide margin. R. & G. AA, with similarly low mildew infection and bolting, was intermediate in yield. The varieties U.S. 14, which showed the highest mildew infection, and Braune and U.S. 23, with intermediate mildew infection and moderately high seedstalk formation, were the lowest in productivity. Data on the effect of time of infection on productivity were not collected from the 1939 trials.

Comparing the three variety plantings conducted in different years, one notes significant differences in the relative susceptibility of varieties. Evidently, however, certain named varieties do not show the same relative sus-

ceptibility or yielding capacity in the different trials. R. & G. Old Type, for example, showed intermediate susceptibility and yield in 1937 and 1938, and intermediate bolting tendency in 1938. In 1939, however, the same variety was low in mildew infection and bolting, but very high in productivity. The same seed lot of R. & G. Old Type used in the 1939 trials had been planted along with four other varieties by the Spreckels Sugar Company in 1938 in a field adjacent to the 1938 mildew plots. Although the other four varieties (U.S. 12, U.S. 14, U.S. 33, and A-600) showed yields of only about 3 tons per acre more in the Spreckels plots, R. & G. Old Type yielded 12.75 tons per acre more than the same variety in the mildew test plots. In the same way the variety Hartmann showed low mildew infection and high productivity in the 1937 trials, but was intermediate in both categories in the 1938 and 1939 trials; and Braune, the highest yielder in 1938, fell below the average of all varieties in 1939. These apparent inconsistencies may be due to interaction of seasonal factors upon disease reaction and varietal productivity, or perhaps may result from variations in the performance of different strains or seed lots distributed under the same variety name. Judging from these results, there are significant differences in the susceptibility of commercial sugar-beet varieties to downy mildew, but similar relative differences occurred when different seed lots of the same variety were planted in different seasons.

TABLE 7

RESULTS OF THE SUGAR-BEET VARIETY TRIALS; SALINAS, 1939*

Variety	Mildew infection, June 23	Bolting, August 10	Sucrose	Yield per acre	
				Beets	Indicated available sugar
	per cent	*per cent*	*per cent*	*tons*	*pounds*
U.S. 15†	13.3	0.3	15.22	51.46	13,010
R. & G. AA	13.6	1.4	14.86	42.37	10,400
R. & G. (Old Type)	14.0	4.1	14.83	52.92	13,030
Eagle Hill 472	15.8	7.1	14.40	45.24	10,480
Glostrup	16.2	12.0	14.60	45.92	10,900
U.S. 23†	17.1	23.0	14.13	39.20	8,880
Eagle Hill 651	17.2	7.1	13.68	46.20	10,120
Hartmann	18.6	11.4	13.85	48.21	10,570
Braune	24.2	15.2	14.48	40.36	9,480
U.S. 14	35.0	11.1	13.12	42.92	8,960
Significant differences:					
Odds 19:1	3.64‡	2.52‡	1.00	2.25	970
Odds 99:1	4.86	3.37	1.34	3.00	1,300

* Planted January 24, 1939; harvested October 11 and 12, 1939.

† Seed furnished by Division of Sugar Plant Investigation, United States Department of Agriculture.

‡ These data have also been converted to degrees and analyzed on the basis of the transformation, $p = \sin^2 \theta$. The conclusions are unchanged except for the bolting tendency of varieties U.S. 15 and R. & G. AA. The transformed data indicate a significant difference between these varieties.

In the single trial in which it was included, variety U.S. 15 showed low susceptibility to downy mildew, low bolting tendency, and high productivity. Variety R. & G. AA appeared to equal it in resistance to downy mildew and showed a low bolting tendency, but exhibited extreme variability in growth habit and was only moderately productive in comparison with other varieties.

U.S. 14 was the most susceptible variety in each of the three trials, while other varieties tested appeared moderately susceptible.

Evidently no commercial variety now available can be considered highly resistant to downy mildew; there is a real need for one combining downy-mildew resistance with favorable agronomic characteristics for planting in the coastal areas of California.

SELECTION FOR RESISTANCE TO DOWNY MILDEW

One can improve the resistance of established varieties by plant selection or by hybridization. Since no highly resistant strain of beets was located, since the commercial strains are highly heterozygous, and since even the strains selected for other characters show considerable differences in susceptibility to downy mildew, it appeared that selections made within acceptable commercial varieties would be most likely to attain the desired objective.

Seedling-Inoculation Method.—At the start of these trials it was not known whether seedling resistance was correlated with field resistance. Since, however, the fungus usually infects only young seedlings or young leaves of older plants, the seedling-inoculation method of selection was chosen.

Large numbers of sugar-beet seed balls of several commercial varieties were planted in chemically or steam-sterilized soils in a greenhouse. After producing their first pair of true leaves, the seedlings were sprayed at intervals of 2 to 5 days with a spore suspension.

The inoculum was prepared according to a method first suggested to the writer by Makato Hiura. Young infected leaves were collected during the afternoon, and the entire coating of conidia and conidiophores was washed off under a spray of water. Then the leaves, having been shaken to remove films or drops of water, were placed in a glass moisture chamber and incubated for 24 hours at 12° or 15° C, temperatures favorable for sporulation of this fungus. By the following afternoon the incubated leaves had usually produced an abundance of conidiophores bearing young viable conidia. Their viability was readily determined by germination trials in water drops on clean slides. Sporulating leaves were placed in a dish containing tapwater; and with a soft brush the conidia were washed and removed from the leaf surface into the water. The concentration of the spore suspension could be judged by its opacity and confirmed by microscopic examination.

Before inoculation the seedlings were moistened with a mist to provide small droplets of water on the leaves. Then the spore suspension was sprayed uniformly over the seedlings with an atomizer or—in larger quantities—with a 1-quart pressure sprayer. After inoculation the beds containing the seedlings were enclosed with muslin-covered frames moistened with a water spray. Plantings were so arranged that inoculations could be made during the season when night temperatures in the greenhouse ranged between 5° and 12° C, temperatures previously found favorable for conidial germination of *Peronospora schachtii* (*4*). For several weeks, similar inoculations were repeated at intervals of 2 to 5 days.

Infection upon seedlings was observed 5 to 10 days after inoculation, depending upon the mean day and night temperatures. As soon as the fungus

had evidently entered the growing point and all newly formed leaves were systemically invaded, the infected seedlings were removed from the beds to provide inoculum for additional inoculations on the surviving seedlings. When 90 to 95 per cent of the seedlings had been eliminated because of infection, the inoculations were discontinued, and the survivors of each variety were transplanted into separate isolation plots. Plantings were usually made in the greenhouse between October 1 and December 1, and the seedlings were transplanted to isolation plots between January 1 and March 1.

Isolation and Seed Production of Selected Plants.—Selections from nonbolting varieties usually produced no seedstalks the first season and were therefore maintained in place until the second summer, when seed was harvested from the selected plants. Among varieties noted for bolting tendencies, from 20 to as high as 70 per cent of the selections produced seedstalks the first season. To avoid, however, additional selection toward a bolting tendency (*1*), the seed from the first-year bolters was discarded except for the small amount that was used for comparative downy-mildew inoculations to test the effect of a single selection on susceptibility in comparison with the parent material. Seed produced the second summer from the remaining plants was used for reselection by the seedling-inoculation method and also for field comparisons under conditions favorable to downy mildew.

Although the plants in a given isolation plot were permitted to cross-pollinate without restriction, conceivably the progeny of certain individual mother plants might differ in resistance from others in the same selection group. The seed from each plant was therefore harvested separately, and then a composite sample from all plants was prepared for large-scale trials while the individual plant progenies were tested separately under downy-mildew exposures. The first selections by the seedling-inoculation method were made in the winter of 1935–36, when 8,650 seedlings were inoculated with spore suspensions of downy mildew nine times within 60 days. A total of 777 seedlings or 8.9 per cent remained uninfected. In the following year 21,472 seedlings were inoculated, and only 313 or 1.45 per cent remained free of infection. The next two seasons, 1937–38 and 1938–39, about 9,000 were inoculated, whereas during the winter of 1939–40 about 25,900 were inoculated, including 15,000 progeny of primary selections made in previous years. In each case a few plants remained free from infection and were saved for increase and reselection. Usually, under natural conditions, field selections of sugar beets for resistance to downy mildew have one disadvantage: the percentages of infection are not high enough to permit rigid selection; and the possibility of selecting susceptible but disease-escaping plants is therefore as great as the chance of picking out truly resistant individuals.

In the 1938 trials near Salinas, however, the field infection was unusually severe; several varieties showed infections of 60 to 80 per cent. Under these conditions a number of mildew-free plants with desirable agronomic characters were selected from each of four commercial varieties. The roots were transplanted into an isolation plot in such a manner that two plants from the same variety grew about 6 inches apart, while adjacent pairs of plants were separated by about 6 feet. When seedstalks were formed, the entire inflorescences of the pair of plants were enclosed in a wooden frame supporting an

insectproof muslin cover. This plan had two advantages: first, it provided sufficient cross-pollination to insure seed production from most pairs of plants, whereas self-sterility often prevents a single-bagged plant from producing seed (*2, 3*) ; and, second, out of twenty pairs selected at random from a given variety, there is a strong possibility of associating two highly resistant individuals in one or more pairs, although other pairs might be composed of one resistant and one susceptible or of two susceptible plants. Inoculation tests upon the progeny are, of course, necessary to distinguish the favorable from the unfavorable combinations.

COMPARISON OF SELECTED STRAINS AND PARENTAL MATERIAL

Greenhouse Evaluation.—The first opportunity to compare the susceptibility of a selected strain with the parent material occurred in the winter of 1937–38. The material originated from the 1936 commercial increase of variety U.S. 33, and the seedlings were heavily inoculated and rigidly selected in the winter of 1936–37. The next summer the seed produced on the first-year bolters was saved, and during the fall of 1937 it was planted in the greenhouse in rows alternating with seed of the parent material. After the first true leaves had been formed on the seedlings, they were sprayed with a spore suspension at intervals of 2 to 5 days. Seventy-five days after planting, 64 per cent of the unselected seedlings were infected, as compared with 37 per cent of seedlings of the primary selection. At the end of 115 days the infection on the unselected and selected strains was 81.4 per cent and 58.8 per cent respectively. Although such trials are less reliable than field comparisons under natural epidemics, the results do indicate that a single selection by the seedling-inoculation method produced a significant difference in susceptibility.

Test at Salinas in 1939.—After elimination of the plants that formed seed stalks during the first year, seed was harvested the following summer (1938) from the remaining plants of the selection mentioned in the paragraph above. This selected seed was planted near Salinas, California, in 4-row strips for observation of its susceptibility and its growth habit. Since not enough seed of the parent strain of U.S. 33 was available for a field planting, comparisons were made with similar plantings of two commercial strains of this variety, one of which was believed to be from the same source as the parent material for this selection.

This trial showed (table 8) that the downy-mildew infection was only one third as severe on the selected material as on the commercial strains closely related to the parental variety. Equally striking was the difference in seedstalk formation between the selection and commercial strains. On May 24, when the commercial strains showed 10.9 and 19.8 per cent bolters, the selection showed only 0.6 per cent seedstalks; and on June 23, when the commercial strains showed 24.4 and 42.6 per cent, the selection showed only 2.3 per cent seedstalks.

In producing seed of this selection, over 40 per cent of the selected plants had been eliminated because they produced seed the first summer; but this elimination could hardly account for the striking effect on the degree and lateness of seedstalk formation. One possible explanation is that in some varieties susceptibility to downy mildew in the seedling stage may be corre-

lated with early bolting, and thus the elimination of over 98 per cent of the most susceptible seedlings may have also eliminated a high percentage of early-bolting individuals. Although definite proof of this possibility is not available, reference to the variety comparisons reported in this paper (table 7) will show that most varieties with low bolting tendencies also show low percentages of downy-mildew infection. Variety U.S. 14, with a moderate bolting tendency and extreme susceptibility to downy mildew, is an exception. The two commercial varieties with the lowest infection, U.S. 15 and R. & G. AA, had been selected not for downy-mildew resistance but for agronomic characters, including a nonbolting tendency; their low susceptibility to downy mildew was discovered after they were released for field trials.

As is shown by the comparative yields of the commercial and selected strains (table 8), early bolting and downy-mildew infection strikingly reduced the

TABLE 8

Comparative Susceptibility of U.S. 33 and a Selection from this Variety, to Infection by Downy Mildew; Salinas, 1939*

Variety	Mildew, June 23	Bolting, August 10	Sucrose	Yield per acre: Beets	Yield per acre: Indicated available sugar
	per cent	*per cent*	*per cent*	*tons*	*pounds*
U.S. 33†	27.9	53.2	9.72	17.09	2,490
U.S. 33‡	27.3	39.3	13.92	21.89	4,830
Selection from U. S. 33†	9.8	16.0	15.08	37.15	9,400

* Planted January 24, 1939; harvested October 11 and 12, 1939.
† From 1936 seed increase.
‡ From 1937 seed increase.

productivity of the commercial strains of variety U.S. 33 when planted as early as January 24, but the selected strain[6] was much less affected by these factors.

Field Plantings in 1940.—In the winter of 1939–40 the progeny of sixteen different selections among five varieties were compared with the parent material by means of greenhouse seedling inoculations. Twelve of the selections appeared to be less susceptible than the parents, while four showed no difference in susceptibility from the source material. Seedlings not infected by the greenhouse inoculations were transplanted to a field near Salinas, to be observed under outdoor conditions. In adjacent rows similar selections were planted from seed along with parental varieties. The most striking evidences of resistance were observed in the progeny from certain individual plant selections, although the progeny of some sister plants from the same selection group appeared to be as susceptible as the parent variety. The individual plant selections also showed striking differences in agronomic characters.

The selections included in these trials originated from five different commercial varieties—three of European origin and two developed in this country by the United States Department of Agriculture.

[6] During the preparation of the manuscript the writer was advised (letter from Dr. Eubanks Carsner, April 24, 1943) that the Division of Sugar Plant Investigations, after extensive evaluation of this selection, has arranged for its multiplication for commercial use.

The European varieties are all susceptible to curly top. Even, therefore, if strains highly resistant to downy mildew could be produced from them, such strains would be useful only for early planting or for planting in areas not seriously affected by curly top.

The highest degree of resistance to downy mildew among the selections, as judged by both greenhouse inoculations and field observations, occurred in a field selection from R. & G. AA increased by the paired-root method previously described. This selection, besides being resistant to downy mildew, showed a strong nonbolting tendency. Being very susceptible to curly top, however, and variable in top and root development, it would be valuable only for reselection or for hybridizing with varieties that possess more favorable agronomic characteristics.

According to observations on the selections from R. & G. Old Type, although some progress has been made in improving resistance to downy mildew, no selection from this source showed sufficient promise to warrant further testing.

Some selections from the variety Hartmann appeared highly resistant to downy mildew. The progenies of two individual plant selections showed only 8.2 and 18.4 per cent infection respectively, as compared with 44.3 per cent infection on commercial Hartmann plants in adjacent rows. These selections, because of their origin, are susceptible to curly top; but in all other respects they offer possibilities.

Selections by the seedling-inoculation method from variety U.S. 14 proved, for the most part, to be nearly as susceptible to downy mildew as the parent variety; there was no evidence that satisfactory strains could be developed in this manner.

The most promising material available at the end of the 1940 season consisted of selections from the curly-top-resistant variety U.S. 33. In table 8 appear the results of a comparison between a mass selection from this source and commercial U.S. 33. According to observations on individual plant selections from U.S. 33, several are much less susceptible to downy mildew than the parent variety, and are also lower in bolting tendency. Additional trials would be necessary to determine whether any of these selections or reselections from them might combine sufficient resistance to downy mildew and other favorable characteristics to be of commercial value.

SUMMARY

Downy mildew reduces the yield of sugar beets by retarding the growth of the root, by interfering with normal sugar production, and by lowering the purity of the beet. Plants showing infection of the growing point before they were 100 days old produced roots about half as large as disease-free plants. Infection on plants over 150 days old, however, resulted in only slight reduction in size.

The sucrose content and the purity of infected beets harvested within 2 months after the termination of a severe mildew outbreak were considerably lower than those of healthy beets. When harvest was delayed for 3 or 4 months after the termination of the epidemic, the sucrose content and the purity were nearly normal. The results of trials during two years indicate that infected beets produce from 30 to 40 per cent less sugar than healthy beets growing in the same field.

Several commercial varieties of sugar beets grown on the Pacific Coast were compared for susceptibility to downy mildew during three years. The most resistant varieties in these tests were U.S. 15, R. & G. AA, and one strain of R. & G. Old Type. Among European varieties some strains or seed lots appeared to be more susceptible than other strains of the same variety.

No varieties were found with enough resistance to provide a satisfactory control for downy mildew.

Selections by the seedling-inoculation method have been made in five commercial varieties. Seedlings growing in a greenhouse during the fall and winter were sprayed repeatedly with spore suspensions of downy mildew. After 95 to 98 per cent of the seedlings were infected, the remainder were transferred to isolation plots for seed production.

Comparison of the progeny of selected seedlings with parental material shows that, in some lines, resistance has been considerably improved.

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CERTAIN SYMPTOMS RESEMBLING THOSE OF CURLY TOP OR ASTER YELLOWS, INDUCED BY SALIVA OF XEROPHLOEA VANDUZEEI

HENRY H. P. SEVERIN, F. DOUGLAS HORN, AND NORMAN W. FRAZIER

CERTAIN SYMPTOMS RESEMBLING THOSE OF CURLY TOP OR ASTER YELLOWS, INDUCED BY SALIVA OF XEROPHLOEA VANDUZEEI[1]

HENRY H. P. SEVERIN,[2] F. DOUGLAS HORN, AND NORMAN W. FRAZIER[3]

INTRODUCTION

In 1938, during an investigation of leafhopper species to determine which were vectors of aster-yellows virus, *Xerophloea vanduzeei* Law., was tested. This insect was at first thought to be a vector, for after feeding on infected asters it produced, in healthy plants, some symptoms closely resembling those of aster yellows. Further preliminary tests, however, showed the same results even when the insect had been reared entirely on healthy asters and was presumably noninfective for yellows. When the insect was tested on sugar beets, it caused some symptoms resembling those of curly top, even though it had not previously been allowed to feed on curly-top-infected plants.

The disease produced by the feeding of this insect is not likely to be of commercial importance on either beets or asters. In twenty-eight years of work on curly top, the senior author has never taken *Xerophloea vanduzeei* on beets in the field, nor observed it on asters under natural conditions. It has been collected, however, in alfalfa fields. Nevertheless, the fact that diseases so closely simulating curly top and aster yellows could be produced when apparently these viruses are not involved suggests that definite identification of these two virus diseases is not possible from symptoms alone. Furthermore, similar situations may exist with other sucking insects or other syndromes. A brief review of the literature follows.

REVIEW OF LITERATURE

Ball (1918)[4] discovered one of the most striking examples of a plant disease, namely hopperburn of potato induced by the potato leafhopper, *Empoasca fabae* (Harris). He (Ball, 1919) concluded that the explanation of the disease was to be found in "some specific transmitted by the insect," and that the production of the disease was specific to the potato leafhopper. Eyer (1922*a*, 1922*b*) and Fenton and Hartzell (1923) attribute the causative agent of hopperburn to some specific substance in the insect's body.

Ball (1919) attributes hopperburn to an "infection or an injection." Whether it will prove to be a specific disease like curly top is yet to be worked out. According to Granovsky (1928) the symptoms indicate the presence of some infective principle or virulent toxin. Johnson (1934) states that the pathological symptoms caused by the potato leafhopper on forage legumes were not due to the transmission of a virus by this insect.

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[4] See "Literature Cited" for complete data on citations, referred to in the text by author and date of publication.

Granovsky (1928, 1930), Monteith and Hollowell (1929), and Poos (1929) suggested that the probable cause of hopperburn was some "chemical or enzymic toxin" injected by the leafhopper into the tissue of the plant, where it remained more or less localized.

Granovsky (1930) reported that a histological study of injured tissue showed a gradual disorganization and granulation of the plastids, clogging of the vascular bundles, and complete disorganization of the phloem region. Microchemical tests revealed a greater accumulation of starch grains and reducing sugars in the tissue injured by the leafhopper. He concluded that these phenomena are evidently due to enzymic secretions in the course of feeding of the leafhopper.

Later investigations by Smith and Poos (1931) and Johnson (1934) have verified the histological changes reported by Granovsky. Smith (1933) and Poos and Wheeler (1934) reported that the clogging or sheath material is secreted by the salivary glands of the leafhopper, is largely protein, and may contain chitin. These authors consider that the injection of some toxic substance into the plant during the feeding of the leafhopper remains a possibility, but it is believed to be improbable. They suggest that an overaccumulation of the carbohydrate products of photosynthesis above the points where a plugging of the vascular tissue is caused by the leafhopper in its feeding upon the veins of the stem tips.

According to Medler (1941), plant injury by *Empoasca fabae* results both from the insect's habit of feeding in the vascular tissue and from the action of a specific compound which is injected during the feeding process and which causes hypertrophy in affected cells. Conceivably, the hypertrophied cells cause an interruption of translocation processes, which initiates secondary external symptoms of chlorosis or reddening in alfalfa leaves.

All investigators of hopperburn agree that the causative agent is localized in the leaves subjected to leafhopper feeding. Fenton (1921), Fenton and Hartzell (1923), and Poos (1929) suggested that the disease was not systemic. Poos and Wheeler (1943), however, proved that it was not systemic by enclosing an alfalfa plant in two cages: the shoots containing potato leafhoppers developed symptoms of the disease, and the shoots free from insects remained healthy.

In China, Wang and Yuan (1924) on the authority of Teng (1931) demonstrated that the leafhopper *Empoasca biguttula* Mats. = (*Chlorita biguttula* Mats.) was associated with crytosis, or clubleaf of cotton. Teng confirmed the causal relation of this leafhopper to the disease, which he suggested may possibly be a direct insect injury or, perhaps, a virus disease somewhat different from the ordinary. Five methods of mechanical inoculation of healthy plants gave negative results. As these writers note, it has not yet been established whether clubleaf of cotton is localized or systemic.

Stigmonose.—Woods (1900) was one of the first plant pathologists who demonstrated that the puncture of the aphid *Rhopalosiphum dianthi* Shrank induced a leaf-spotting disease of carnations and other pinks. He concluded that the "insect injects some irritating substance of an acid or enzymic nature in the wound, and that this substance causes the increase of oxidizing enzymes in the cells which it reaches, and that these enzymes interfere with

the nutrition of the cell destroying the chlorophyll and setting up other changes which finally result in death."

Froghopper Blight of Sugar Cane.—Froghopper blight of sugar cane is caused by the feeding of a cercopid, or froghopper, *Thomaspis saccharina* Dist., and has been studied intensively by Williams (1921) and Withycombe (1926). The effects of the sucking of the froghopper are the removal of water, carbohydrates, proteins, and so forth, and the injurious effects on the border parenchyma. The injurious effects of the saliva are accomplished partly by diastatic and oxidizing enzymes. Oxidases of the plant and the saliva seem to be responsible for the color changes and production of red pigment; but more important is their effect upon the H-ion concentration of the cell sap. Increase in transpiration may occur locally after puncture, the phloem becomes blocked, translocation is inhibited, and the metabolic equilibrium of the plant is upset. A local lesion is followed by systemic effects.

Mealybug Wilt of Pineapple.—According to Carter (1932) this disease is induced by a diffusable, systemic, toxic secretion injected into the plant by the feeding of the pineapple mealybug, *Pseudococcus brevipes* (Ckl.). There is no evidence for multiplication of the toxin in the plant, and recovery from wilt is commonly encountered. Evidence of antitoxic reactions on the part of the plant is available. The toxicity of a mealybug colony varied according to the host plants from which it was transferred, including the roots of grasses, and was intensified in succeeding generations reared on pineapples (1939). This is believed to result from changes in the insects' secretion, induced by the varied nutritional conditions afforded by the host plants.

Green Spotting of Pineapple.—Carter (1933) has shown that the pineapple mealybug, *Pseudococcus brevipes* (Ckl.), causes two types of spotting on pineapple leaves. One is chlorotic, and the other is a different type known as green spot. Colonies of mealybugs produce green spots on leaves at the point of feeding, and this ability when present in adult females was transmitted to the young; but this capacity was absent in mealybugs from the roots of certain grasses. Green spotting is not a symptom of pineapple wilt, but is a local, toxic effect of the feeding of a strain of *P. brevipes.* Mealybugs that induce green spots are dark gray, this shade being caused by the presence of a dark-colored mycetome; on the other hand, pinkish-gray forms do not cause green spotting. According to Carter (1936, 1939), in Hawaii the symbiont flora in the mycetome of the mealybug is clearly associated with the ability to produce green spots.

Ito (1938) found 2 strains of *Pseudococcus brevipes:* the gray form, which causes green spotting, reproduced sexually, producing both males and females, whereas the nongreen spotting form reproduced parthenogenetically, producing only females.

Psyllid Yellows.—Psyllid yellows is produced only by the nymphs of *Paratrioza cockerelli* Sulc.; the adult is incapable of producing the disease. Binkley (1929) concluded that the disease was caused by a virus. Shapovalov (1929) observed what he thought was tuber transmission of the disease in potato, but Richards and Blood (1933) failed to transmit psyllid yellows through the tuber. According to Richards and Blood, the most plausible explanation of the cause of the disease is as follows: the nymphs during their feeding process

inject into the plant tissue some toxic substance; this quickly becomes systemic and possibly produces the exaggerated responses characteristic of the disease by interfering in some way with the carbohydrate metabolism of the plant.

Anasa Wilt of Cucurbits.—According to Robinson and Richards (1931), squash and pumpkin growing had been completely abandoned in many parts of Utah owing to a peculiar wilt which is caused by the feeding of the squash bug, *Anasa tristis* DeG. Wilting results in 1 to 16 days, the time depending upon the age of the plant, the progress of the season, and the number of insects feeding. Wilting results only above the point of insect contact, whether the petiole or the entire stem is exposed to feeding. When wilting is not too complete, plants uniformly recover upon the removal of the insects. These workers suggest the possibility that a toxic substance injected by the insect during the process of feeding is involved.

In 1938 an investigation was undertaken to learn the nature of the injury caused by the feeding of *Xerophloea vanduzeei*—whether it is a virus disease, a mechanical injury, or the effect of a toxic secretion by the insect. The life history of the insect was studied. The symptoms of the disease on sugar beet and on aster were observed in detail, and experiments were performed to determine whether the effects were local or systemic. Tests were made to transmit the disease from affected plants to healthy beets or asters by known curly-top or aster-yellows vectors and by mechanical inoculation. There were further attempts to ascertain whether this species is a vector of the curly-top and aster-yellows viruses.

MATERIALS AND METHODS

The production of noninfective beet leafhoppers, *Eutettix tenellus* (Baker), was first described by Stahl and Carsner (1918) and Severin (1930); that of noninfective short-winged aster leafhoppers, *Macrosteles divisus* (Uhl.), and long-winged aster leafhoppers, a race of the same species, by Severin (1929*b*, 1940, 1942).

The preparations of plant extracts and centrifugation have been described by Severin and Freitag (1933).

One method of mechanical inoculation used is that described by Rawlins and Tompkins (1936). Shortly after inoculation the carborundum was washed from the leaves with water. The flamed-needle method of inoculation with a cotton swab near the point was also employed (Severin, 1924).

DISTRIBUTION, FOOD PLANTS, AND LIFE HISTORY OF XEROPHLOEA VANDUZEEI

The genus *Xerophloea*, erected by Germar in 1839, belongs to the subfamily Gyponinae. According to Lawson (1931), color and genitalia are of little or no value in the identification of this genus. The shape of the vertex and the degree of inflation of the front are dependable characteristics. These, along with size and geographical distribution, were sufficient to enable a proper differentiation of the several species.

In its geographical distribution, *Xerophloea vanduzeei* is limited to California.

The species was commonly collected on Australian saltbush (*Atriplex semi-*

baccata) in the Imperial, Salinas, and San Joaquin valleys. It has also been taken on weeds growing in grain stubble fields in the Sacramento and Santa Clara valleys. Specimens were also captured on nettleleaf goosefoot (*Chenopodium murale*) and rough pigweed (*Amaranthus retroflexus*) in Los Angeles County, puncture vine (*Tribulus terrestris*) and a burweed (*Franseria acanthicarpa*) in Tulare County, and yellow star thistle (*Centaurea solstitialis*) in Sonoma County. Among economic plants it has been taken on alfalfa, grapevines, and vetch.

Oviposition.—Under greenhouse conditions the ovipositing female cuts an incision in the petiole, midrib, or lateral veins of the sugar-beet leaves and

TABLE 1

Duration of Nymphal Stadia of *Xerophloea vanduzeei*

Sex and date hatched	Duration of stadia						Total
	1st instar	2d instar	3d instar	4th instar	5th instar	6th instar	
	days	*days*	*days*	*days*	*days*	*days*	*days*
Males:							
April 28	16	10	5	9	11	..	52
April 22	15	12	9	9	13	..	57
April 14	11	12	9	8	18	..	58
April 19	14	11	8	12	13	..	58
April 26	15	12	9	9	14	..	61
April 12	14	13	11	11	16	..	65
Average	*12.7*	*10.8*	*8.5*	*9.8*	*14.2*	..	*58.3*
Females:							
April 22	15	14	13	14	10	..	65
April 14	14	15	13	14	10	..	66
April 22	17	12	10	11	17	..	67
April 12	17	9	11	15	15	..	67
April 28	12	13	10	9	14	12	70
April 28	16	10	18	13	17	..	74
Average	*15.1*	*12.1*	*12.5*	*12.7*	*13.8*	*12.0*	*68.2*

embeds a single egg in this slitlike chamber. Oviposition in the field has not been observed by the present authors.

Egg.—The egg after deposition averages 2.75 mm long, 0.5 mm wide. It is elongated, narrower at one end than at the other, with the dorsal and ventral surfaces differently curved. As the hatching period draws near, the anterior pole may protrude from the mouth of the egg chamber, and the pink eyes of the embryo may be visible. After hatching, the eggshells usually protrude from the mouth of the egg chambers or are pulled out of those chambers and adhere to the petiole, midrib, or veins.

The slitlike incision turns brown after the egg is embedded in it, black after the egg hatches. When successive eggs are deposited in rows, the petiole sometimes cracks so that the eggs fail to hatch.

Duration of Stadia.—Table 1 indicates the duration of the nymphal stadia. The total duration of these stadia in the males is shorter than in the females. One nymph, a female, passed through six molts; all others through five.

Measurements of Instars.—Table 2 gives the average measurements of various parts of the body 1 day after hatching and 1 day after each molt. The

diameter of the head was measured across the compound eyes, and its length along the dorsal median line. As table 2 indicates, each instar can be determined accurately by the diameter and length of the head and the length of the abdomen. Average measurements of the male and female leafhoppers that completed five molts show the males to be smaller than the females. The pink females are larger than the cream, and the cream larger than the green.

Color of Nymphal Instars.—The first nymphal instar after hatching is white, later gray (plate 1, *A*). The thorax and abdomen are covered with numerous hairs. The second instar is greenish gray (plate 1, *B*). The third, fourth, and fifth instars become progressively greener (plate 1, *C, D, E*).

TABLE 2

COLOR AND AVERAGE MEASUREMENTS OF NYMPHAL INSTARS AND ADULTS OF *Xerophloea vanduzeei**

Nymphs and adults	Width of head	Length of head	Length of head and abdomen	Length to end of wings	Color
	mm	*mm*	*mm*	*mm*	
Nymphs:					
First instar	0.56	0.39	1.42	....	Gray
Second instar	0.81	0.55	2.08	....	Greenish gray
Third instar	1.11	0.77	2.83	....	Green
Fourth instar	1.47	1.00	3.92	....	Green
Fifth instar	1.92	1.21	5.36	....	Green
Adults:					
Male	1.83	0.69	5.46	5.79	Brown
Female	2.04	0.90	6.31	6.39	Green
Female	2.10	0.88	6.41	6.62	Pink
Female	2.02	0.85	6.46	6.52	Cream

* Ten insects measured for each average.

Color of Adults.—There are four color forms of adults—brown males and green, pink, and cream-colored females (plate 1, *F, G, H, I*). Green females that acquired the winged stage on July 3, had faded to a straw color by September 18, when the next observation was made; but the head and the thorax were still a faded green. The cream form is different from the straw; the cream females appear immediately after the last molt. The female offspring of single females of each of the three color forms are usually green or cream, rarely pink; evidently, therefore, the three color forms of females belong to the same species.

DESCRIPTION OF SYMPTOMS

On Sugar Beet.—The succession of symptoms on the sugar beet, *Beta vulgaris*, resulting from the feeding of 20 or more nymphs or adults is not always constant; hence each symptom will be described more or less independently of the varying sequence.

The first symptom appearing on the youngest leaves of beet seedlings may be a clearing of the veins and veinlets (plate 2, *A*), which usually begins as a small area on one or both sides of the midrib at the basal portion of the blade, and later spreads as a network over most of the leaf. There may be an inward rolling of the margin of the youngest leaves (plate 2, *D, E*), accompanied by

cleared veinlets and protruding veins. These symptoms resemble those produced by the curly-top virus on the youngest leaves of sugar beets (Severin, 1929*a*).

The veinlets on the lower surface of the youngest leaves swell prominently, and the midrib and lateral veins protrude (plate 2, *B*). Protuberances may appear on the upper surface of the leaves (plate 2, *C*), whereas in curly-top small wartlike elevations develop on the veins on the lower surface of the leaves (Severin, 1929*a*).

Part of the leaf becomes yellow, sometimes near the tip (plate 3, *B*), along one or both sides of the midrib (plate 3, *C*), or on the basal portion of the blade (plate 3, *A*). The yellowing is characteristic of the older leaves. Within 1 or 2 days the yellow area becomes dry, resembling a "burning" of the tissue (plate 3, *C, D, E*). The yellowing spreads and is followed by drying; usually the leaf dies within 4 to 8 days. Necrosis of the midrib and veins sometimes appears when the blade is chlorotic (plate 3, *D*). Yellowing and drying are not limited to the older leaves; the intermediate and younger leaves may also be affected. On the youngest leaves, which are more resistant, yellowing usually does not spread over more than a small area of the blade. When two or more insects feed on the petiole of an older leaf, yellowing usually appears on the blade before the cleared veinlets occur on the youngest leaves. After the symptoms first appear on either the youngest or the older leaves, the intermediate leaves become affected, and finally most of the leaves show one or more types of the symptoms described. When the nymphs or adults were removed from the beets, the newly developing leaves were normal.

Some sugar beets may develop several types of malformed leaves. The midrib may be curved (fig. 1, *A*) near the tip of the youngest leaves and near the base of the older leaves. The leaves may be asymmetrical (fig. 1, *B*); one half of the blade may be narrower than the opposite half (fig. 1, *B*) with an outward rolling of the margin of the dwarfed side. The basal margin of the leaf may be rolled inward (fig. 1, *C*). Sometimes the leaves assume a rectangular form, with or without cleared veinlets, and usually with protuberances on the upper surface of the blade.

On China Aster.—The first symptom on the youngest leaves of the China aster, *Callistephus chinensis*, is a clearing of the veins and veinlets (plate 4, *A, B*), which is more sharply defined than that induced by the aster-yellows virus (plate 4, *C, E*). Pale-yellow veinbanding, indistinguishable from that caused by the aster-yellows virus, develops later. The transparent veins appeared on the youngest leaves within 1 to 14 days after the nymphs were caged on the plants and within 3 to 32 days when adults were used (table 3), whereas the incubation period of aster yellows varies from 11 to 27 days and averages 18 (Severin, 1929*b*). After the nymphs or adults were removed from the asters, the newly developing leaves failed to show symptoms.

Sometimes the youngest leaves show small, interveinal, green, blisterlike elevations (plate 5, *C*); on many host plants the viruses of common cucumber mosaic, western cucumber mosaic, and celery calico produce elevations similar to these, but not necessarily interveinal. The youngest leaves may be asymmetrical, and pale-yellow veinbanding may occur along the cleared veins and veinlets (plate 5, *A, B, C*).

Normal elongation of the internodes is inhibited by the causative agent, and the aster plant becomes dwarfed. Axillary shoots develop from the bud in the axils of the leaves (plate 5, *D*), as in aster yellows. Cleared veins and veinlets and pale-yellow veinbanding appear on the involucre bracts and intermediate leaves (plate 5, *D*). The veinbanding on the bracts of the apical buds fades

Fig. 1.—Sugar beet (*Beta vulgaris*): *A*, malformed leaf with curved midrib; *B*, asymmetrical leaf with outward rolled margin; *C*, basal margin rolled inward, induced by the causative agent of *Xerophloea vanduzeei*.

just before the buds begin to expand, and nearly all the axillary shoots become chlorotic.

The involucre bracts may be dwarfed, malformed, and asymmetrical; sometimes the midribs of the older bracts are curved or twisted (plate 6, *A*, *B*). The bracts may be linear (plate 6, *A*, *B*). Growth is slower in the part of the bract showing cleared venation.

The apical flower bud is somewhat reduced in size; and frequently the petals are curled outward or twisted in a corkscrew (plate 6, *D*). The buds on the axillary shoots expand only partly or not at all and are dwarfed (plate 5, *D*).

Sometimes only part of a bud may open, and the petals may be small and twisted (plate 6, *C*). Virescence or greening of the flowers may occur—sometimes on only a portion of the flower, the remainder retaining the normal color, as in aster yellows (plate 7).

The most striking symptom induced by the leafhoppers' feeding is the breaking in color of the petals. When the leafhoppers are caged on an aster plant in the late bud stage, the bud expands into a large flower, and the petals begin to break in color (plate 8, *A*). The breaking consists of white streaks alternating with the normal color of the flowers. The white streaks encompass only the parallel veins at first when examined under a binocular microscope, but soon spread out on each side of the vein. Even if the leafhoppers are removed from the plant, the white gradually becomes more profuse (plate 8, *B*), and the normal color becomes less and decreases in intensity. Certain of the petals are rolled; others are twisted, sometimes in a spiral (plate 8, *D*).

ATTEMPTS TO TRANSFER CAUSATIVE AGENT FROM DISEASED PLANTS AND LEAFHOPPERS

By Beet and Aster Leafhoppers.—No success was achieved in attempts to recover a causative agent from sugar beets showing symptoms induced by *Xerophloea vanduzeei* and to transfer it to healthy beet seedlings by means of 5 lots of 20 noninfective beet leafhoppers. Likewise, 5 lots of 20 noninfective short-winged and 5 lots of 20 long-winged aster leafhoppers, after feeding on asters showing symptoms, failed to produce symptoms on healthy asters to which they were transferred.

By Mechanical Inoculation.—Only failures resulted from mechanical inoculation with carborundum of the leaves and petioles of 25 healthy beet seedlings and 25 asters with sap extracted from beets and asters that showed symptoms. Inoculations of the midrib and petioles of 10 healthy beet seedlings and 10 asters, using a flame needle with a cotton swab near the point, were also negative. On the other hand, when beets were inoculated with the flamed needle in the crown between the bases of the petioles, the characteristic yellowing and necrosis of the outer leaves developed. No symptoms appeared on the younger leaves. Controls inoculated with sterile distilled water remained healthy. This method of inoculation of the crown of healthy sugar beets with the virus extract from curly-top beets was also successful in the production of this disease (Severin, 1924).

By Salivary Glands.—The salivary glands of each of 10 nymphs crushed in a puncture of each beet root between the bases of 2 petioles by the flamed-needle method of inoculation, induced yellowing and necrosis of one or more outer leaves.

By Noninfective Nymphs.—Nymphs of *Xerophloea vanduzeei* were transferred singly during the process of hatching from a sugar beet before feeding to a healthy aster; the cleared veinlets appeared on the youngest leaf in 4 to 12 days. This experiment eliminates a virus as the causal agent unless it may be argued that a virus passes through the egg.

FAILURE TO RECOVER CURLY-TOP AND ASTER-YELLOWS VIRUSES

Nymphs and adults of *Xerophloea vanduzeei* that completed the nymphal stages on curly-top beets or infected asters were allowed to feed on healthy beet seedlings and asters respectively. In these healthy plants, lots of 20 noninfective beet leafhoppers and short-winged and long-winged aster leafhoppers failed to recover the viruses and transfer them to 5 healthy beet seedlings and 10 asters.

SYSTEMIC NATURE OF CAUSATIVE AGENT

An experiment was carried out to ascertain whether the causative agent is systemic. Eight lots of 10 leafhoppers were confined in cellophane cages enclosing a single leaf. Four beet seedlings and four asters were used. One lot of nymphs and one lot of adults were confined on the outer leaves, and one lot of each stage on the inner leaves, of each kind of plant. If a leaf died, the cage was transferred to another similar leaf of the same plant. Two beet seedlings and two asters were used as checks; each was enclosed by a large lawn-covered cage containing either 10 nymphs or 10 adults, the insects being allowed to feed on all portions of the plant except the roots. The experiment was continued for 20 days.

By the eighth day, cleared veinlets of the youngest leaves had appeared on one aster and faintly on one beet seedling, both plants being ones which had leafhoppers on an inner leaf. By the twentieth day, however, all beets and asters showed symptoms. The fact that symptoms developed on the youngest leaf when the insects had fed on an outer leaf indicates that the effect is systemic.

Another method was used to demonstrate the systemic effect of the active principle in asters. A single nymph was confined in each leaf cage (Severin, 1924), which was clamped to a petiole of a basal leaf, in total numbers varying from 1 to 5 on each plant. One case in which 2 nymphs were used per plant will suffice to show the rate of travel of the inciting agent in the aster. In a plant with 2 nymphs the cleared venation appeared within 3 days on an axillary shoot below the petioles on which the nymphs were feeding. The next day the symptom developed on the intermediate axillary shoots; the following day, on the apical shoot; and one day later, on the involucre bracts below the apical flower bud. In one aster plant cleared venation appeared on the leaves of an intermediate axillary shoot above the petiole on which the nymph was feeding, followed by cleared veinlets on the leaves of the next lower secondary shoot. Sometimes the toxic effect produced cleared veinlets on the axillary shoots on one side of the aster, and on the opposite side normal shoots developed. Breaking in the color of the petals appeared after the flower bud expanded and also on flowers of the axillary shoots. Similar results were obtained with the 3 other plants, but the time required for the symptoms to develop on the leaves of the axillary shoots was longer. Seventeen aster plants failed to develop cleared venation, but breaking in color of the flowers occurred.

INCUBATION PERIOD OF DISEASE

Nymphal Instars and Adults.—The incubation period of the disease produced by each instar was compared with that induced by the adults. Twelve insects were tested throughout their life history, a healthy aster being provided for each instar and successive asters for each adult as rapidly as symptoms developed. One female failed to induce the disease during adult life. Table 3 shows the results obtained. The average time for symptoms to develop was less for every nymphal instar than for the adult.

TABLE 3

TIME REQUIRED FOR DEVELOPMENT OF FIRST SYMPTOM ON ASTERS INDUCED BY FEEDING OF NYMPHAL INSTARS AND ADULTS OF *Xerophloea vanduzeei*

Sex and insect no.	Time required for cleared venation to develop							
	1st instar	2d instar	3d instar	4th instar	5th instar	6th instar	Adults	Average
	days	*days*	*days*	*days*	*days*	*days*	*days*	*days*
Males:								
No. 1	8	1	..	3	4	..	12, 4, 6, 15	9.2
No. 2	14	11	6	..	5	..	3, 6, 9, 6, 8, 10, 18, 32	11.5
No. 3	9	4	4	6	3	..	5, 4, 3, 5	4.2
No. 4	10	5	4	4	..	..	7, 4, 7, 7, 7, 10, 20	8 9
No. 5	..	5	3	2	2	..	5, 7, 4, 4, 5, 12	6.2
No. 6	6	4	8	5	..	..	5, 5, 28, 16, 6, 15	11.5
Average	*7.8*	*5.0*	*4.2*	*3.3*	*2.5*	..		*8.6*
Females:								
No. 1	..	3	5	7	3	..	19, 9	14.7
No. 2	..	3	4	3	2	..	22, 5	13.5
No. 3	7	..	..	..	6	..	*	....
No. 4	8	3	4	7	3	..	6, 5. 3	4.6
No. 5	..	13	3	..	6	6	5, 6, 5, 5, 5, 8, 8, 5, 15. 4, 5, 6, 7	6.5
No. 6	8	3	4	5	4	..	5, 6, 14	8.3
Average	*3.6*	*4.2*	*3.3*	*3.7*	*4.0*	*6.0*		*7.3*

* Insect failed to induce the disease during adult life.

Overwintering Adult Color Forms.—The adult color forms that wintered over in the greenhouse on asters were transferred singly to healthy asters to determine whether there was any difference in the incubation period of the disease. Two or 3 females of each color form were used. Only 1 male was studied in the experiment. The number of days required for the cleared venation to appear on asters with each color form was as follows:

Green females: No. 1—40, 7, 6 days, No. 2—33 days. No. 3—23 days. Average, 21.8 days.

Pink females: No. 1—9, 11, 10, 19, 6 days. No. 2—17, 11, 5, 6 days. No. 3—23 days. Average, 11.7 days.

Cream females: No. 1—43 days. No. 2—29 days. Average, 36.0 days.

Brown male: 13, 18, 5, 5, 8, 8, 7, 5, 4, 5, 11, 7. Average, 8.0 days.

SUMMARY

The eggs were deposited in the petioles, midrib, and veins of sugar-beet leaves. One nymph passed through six molts; all others through five. Each instar can be determined accurately by measurements of the head across the compound eyes. The color of the first instar is gray; of the second, greenish gray; and of the third, fourth, and fifth instars, green. The adults have four color forms—namely, gray males and green, pink, and cream-colored females.

On sugar beets the feeding of *Xerophloea vanduzeei* induces cleared veinlets, previously considered a reliable symptom of curly top. On asters it induces cleared venation with yellow veinbanding, stunting of the plants, development of axillary shoots from the bud in the axil of the leaves, and virescence of the flowers, all symptoms of aster yellows. The most striking effect produced by the feeding of the leafhoppers is breaking in the color of the petals.

Only failures resulted from mechanically inoculating the leaves, midrib, and petioles of healthy beet seedlings and asters, using carborundum or a flame needle with a cotton swab near the point. When beets were inoculated with the flamed needle in the crown between the bases of the petioles, the characteristic yellowing and necrosis of the outer leaves developed. No symptoms appeared on the younger leaves.

The salivary glands of each nymph that was crushed into a beet root by the flamed-needle method induced yellowing and necrosis on one or more outer leaves.

Known vectors of curly top and aster yellows failed to transmit the causative agent from plants showing symptoms of *Xerophloea vanduzeei* injury to corresponding healthy plants.

In both sugar beets and asters the active principle is systemic and is presumed to be due to a toxic salivary secretion.

The average time for symptoms to develop on asters was less for every instar than for the adult, and longer for three color forms of overwintering females.

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PLATES

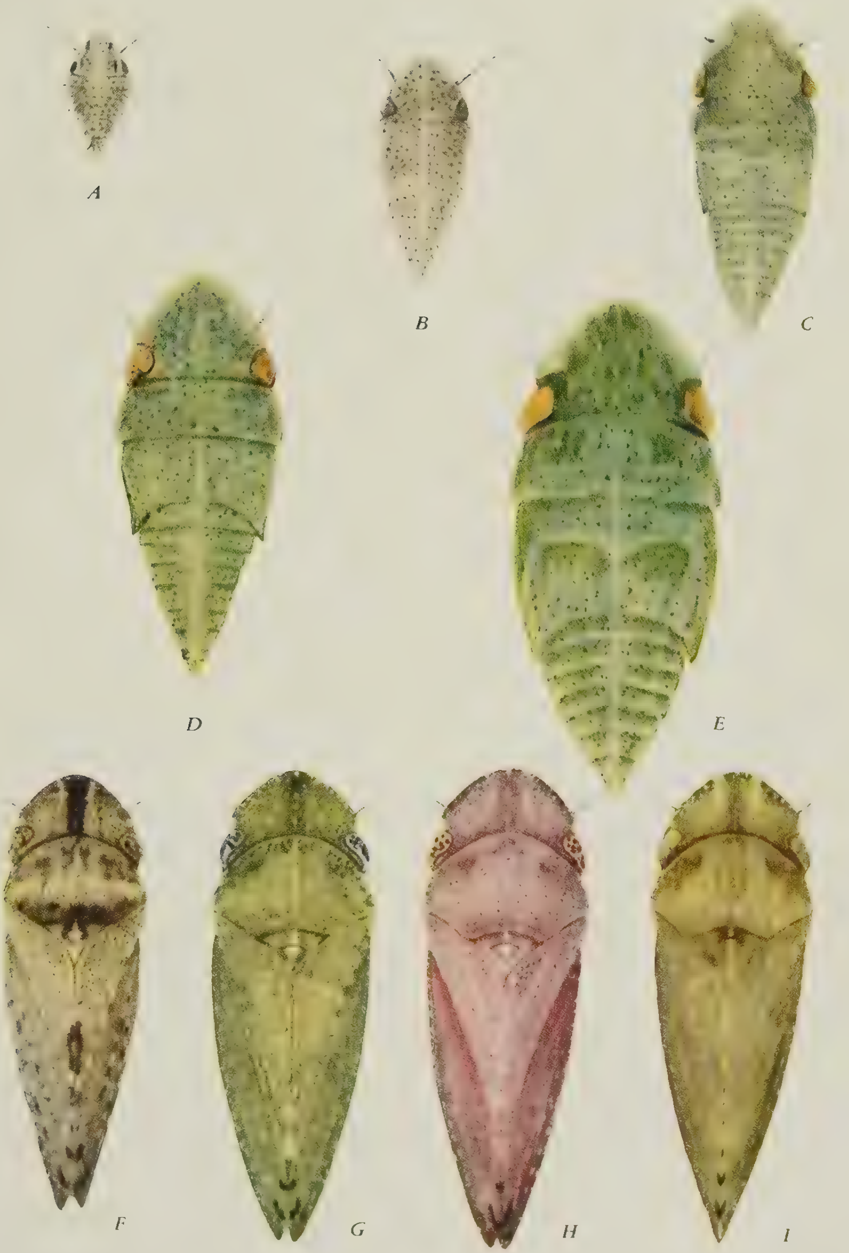

Plate 1.—Color patterns of nymphal instars and adults of *Xerophloea vanduzeei* Law.: *A*, first instar, gray with numerous hairs on thorax and abdomen; *B*, second instar, greenish gray; *C*, *D*, *E*, third, fourth, and fifth instars, green; *F*, adult male, brown; *G* to *I*, adult females—green, pink, cream. (*A*, photographed 1 day after hatching; the others, 1 day after the molt.)

Plate 2.—Sugar beet (*Beta vulgaris*): *A*, younger or inner leaf showing cleared veins and veinlets; *B*, swelling of veinlets, with protruding midrib and lateral veins on the lower surface of the blade; *C*, interveinal protuberances on the upper surface of the blade; *D*, inward rolling of the margin of the youngest leaf and cleared veinlets; *E*, inward rolling of the margin and curved midrib.

Plate 3.—Sugar beet (*Beta vulgaris*): *A*, *B*, *C*, yellowing of basal and apical portions of blade and parts along both sides of the midrib; *D*, necrosis of midrib and veins; *E*, dried basal and middle portion of blade, with apical part still green.

Plate 4.—China aster (*Callistephus chinensis*): *A*, *B*, cleared veins and veinlets induced by toxic secretion of *Xerophloea vanduzeei*; *C*, leaf from healthy check or control plant; *D*, *E*, cleared venation caused by the aster-yellows virus.

Plate 5.—China aster (*Callistephus chinensis*): *A*, cleared veins and veinlets, asymmetrical leaves; *B*, cleared venation with yellow veinbanding; *C*, left, two leaves showing asymmetry and pale-yellow veinbanding; right, small, green, interveinal, blisterlike elevations; *D*, axillary shoots showing pale-yellow veinbanding or chlorotic involucre bracts and intermediate leaves.

Plate 6.—China aster (*Callistephus chinensis*): *A*, axillary shoot showing pale-yellow veinbanding and curved or twisted linear bracts; *B*, axillary shoot showing chlorotic involucre bracts and intermediate leaves near the basal region; *C*, small flower buds with small, twisted petals; *D*, flower with petals curled outward or twisted in a spiral.

Plate 7.—China aster (*Callistephus chinensis*): center, normal flower from a check or control plant. Grouped around it are eight abnormal flowers from aster plants infected with aster yellows, some showing greening of the flowers and others having a portion of the flower green or white while the remainder retains the normal color of the variety.

Plate 8.—China aster (*Callistephus chinensis*): *A*, flower showing breaking in color induced by the causative agent of *Xerophloea vanduzeei*; *B*, five petals showing breaking in color, with white streaks alternating with the normal color; *C*, three petals from healthy check or control plant; *D*, four petals showing rolling or twisting, sometimes in a spiral; *E*, four linear petals.